

# ESTIMATING SOME EARLY LIFE HISTORY PARAMETERS IN A TROPICAL CLUPEID, *HERKLOTSICHTHYS CASTELNAUI*, FROM DAILY GROWTH INCREMENTS IN OTOLITHS<sup>1</sup>

SIMON R. THORROLD<sup>2</sup>

## ABSTRACT

Growth increments in otoliths were used to estimate the age of larval *Herklotsichthys castelnaui*, a tropical clupeid, collected from Townsville, northeastern Australia, in spring/summer of 1987. Daily periodicity of increment formation was confirmed by treating larvae with tetracycline and examining otoliths after a known time period. Initial increments were assumed to form at hatching; ages were thus minimum estimates.

Laird-Gompertz and von Bertalanffy growth models fitted the resultant length-at-age data equally well; therefore, only the Laird-Gompertz model is presented. Specific growth rates declined from 7.4% of standard length per day at 4–5 days old to 0.4% of standard length per day at metamorphosis, 45–50 days after hatching. Absolute growth rates also declined, from 0.6 mm per day at 4–5 days to 0.08 mm per day at 44–45 days. Initial absolute growth rates are as high as any reported for clupeid larvae in the field; after this initial burst, however, the growth trajectory appeared similar to those reported for herring and pilchard larvae in temperate waters.

Spawning periodicity of *H. castelnaui* during the sampling period was determined by examining temporal distribution of birthdates from otolith-aged larvae. There was indication of semilunar peaks in spawning activity, apparently associated with quarter moon phases.

A central problem in fisheries research is understanding mechanisms determining year-class strength. Evidence suggests that regulation of year classes occurs during the early life history of most fish species (Parrish 1973; Smith 1985), and attempts to account for recruitment variability have focussed on this period of the life cycle (e.g., Hjort 1914; Cushing 1975; Koslow et al. 1987). Growth has been established as a critical parameter in the survival and subsequent recruitment of larval marine fishes (Houde 1987). Weight gains of orders of magnitude during larval life suggest a potential for extremely variable growth trajectories which may be reflected in a concomitant variability in survivorship. Growth rates are intrinsically related to susceptibility to both starvation (Lasker 1981) and predation (Rothschild and Rooth 1982). Small changes in growth rate can also have a dramatic effect on recruitment by determining stage durations over which high mortality indices may operate (Houde 1987).

Length-frequency methods have been used exten-

sively to estimate growth in larval fishes, but growth curves generated by this technique may be biased by age- and cohort-specific changes in growth rates (Crecco et al. 1983). Protracted spawning seasons may further complicate growth estimates because of the difficulties associated with connecting length modes in polymodal length-frequency distributions (Lough et al. 1982). Modal progression can also only provide mean growth estimates for larval populations. These estimates are often averaged over months or years, whereas the relevant temporal scale for critical life history events may be hours or days (Fortier and Leggett 1985).

The accuracy and precision of growth estimates for larval fishes have been greatly enhanced by the discovery of daily incremental rings in the otoliths of some fishes (Pannella 1971; see Campana and Neilson 1985; Jones 1986 for recent reviews). Ageing by counting otolith growth increments allows a direct measure of length-at-age for calculation of growth curves and may provide information on individual age and growth rates. Growth estimates have been obtained from a variety of species in this manner (e.g., Struthsaker and Uchiyama 1976; Methot and Kramer 1979). Back-calculation of daily rings may reveal temporal distribution of birthdates (Townsend and Graham 1981; Methot 1983), and

<sup>1</sup>Contribution No. 447 from the Australian Institute of Marine Science, Queensland, Australia.

<sup>2</sup>Australian Institute of Marine Science, P M B No. 3 Townsville M.S.O., Queensland 4810, Australia.

has allowed both temporal and spatial variability in daily growth rates to be investigated (Graham and Townsend 1985; Thomas 1986; Leak and Houde 1987).

Although temperate clupeid species have been the focus of considerable scientific attention (Blaxter and Hunter 1982), the diverse assemblage of heavily exploited clupeids of the tropical Indo-Pacific remain poorly understood (Longhurst 1971; Whitehead 1985). There is a limited selection of literature available on the Indian oil sardines (*Sardinella aurita* and *S. longiceps* (e.g., Nair 1959; Raja 1970)), but these species are not a conspicuous component of nearshore fish communities in tropical Australia (Whitehead 1985). Williams and Clarke (1983) have examined growth in juvenile and adult *Herklotsichthys quadrimaculatus* from Hawaii using the otolith increment technique. A. I. Robertson (MS in prep.) has used length-frequency data to estimate growth in juvenile *Herklotsichthys castelnaui* and *Sardinella albella* from mangrove nursery areas in tropical northeastern Australia. Dayaratne and Gjosaeter (1986) analyzed age structure of juveniles and adults in four species of *Sardinella* from Sri Lanka using daily growth increments on otoliths. Relatively few studies have measured larval age and growth in field situations; these parameters have not been reported for any tropical clupeid species.

In this paper, I examine daily increments in otoliths to determine some early life history parameters of a common clupeid of tropical northeastern Australia. *Herklotsichthys castelnaui* (*Harengula abbreviata* of many authors) is a coastal pelagic clupeid found along the eastern seaboard of Australia from Bloomfield (lat. 15°56'S) to Pambula (lat. 36°57'S; Whitehead 1985). Although little is known of the biology of *H. castelnaui*, it inhabits estuaries and inlets (Robertson and Duke 1987), spawning in summer (January–March) in the southern parts of its range (Blackburn 1941), but probably earlier in the year in more northern areas (Robertson, MS in prep.). There is no information available on larval biology.

The specific aims of this project were to

- 1) validate daily growth increments in the otoliths of larval *H. castelnaui*,
- 2) obtain estimates of daily growth for larvae in the field,
- 3) investigate relationships between otolith size, standard length, and age, and
- 4) determine the frequency distribution of larval birthdates during the spawning season.

## METHODS

### Collection of Larvae

Larvae were collected weekly from Breakwater Marina, Townsville, Australia (Fig. 1) during August to November 1987. The marina is some 5.2 hectares in area, with an average water depth of 5 m (mhw), and is connected to Cleveland Bay by a 30 m wide entrance. Water is flushed in and out of the marina during the normal tidal cycle. Cleveland Bay is shallow, approximately 25 km wide, and bounded by Magnetic Island on its eastern side (Fig. 1). Physical oceanographic parameters of the bay have been described by Walker (1981a, b).

Sampling was conducted at night using three fluorescent lamps sealed within a clear perspex tube and a 1 m × 250 μm mesh size plankton net. The lamps were switched on and the tube lowered into the water from a jetty to a depth of 1.5 m. The plankton net was then lowered approximately 3 m below the tube. The lamps were left on for 15 minutes, then the plankton net was hauled rapidly up over the perspex tube to the surface. This sequence was repeated 4 times during a sampling night at hourly intervals commencing at 20:00.

Almost all larvae were alive upon net retrieval and were transferred immediately into 98% ethanol for subsequent sorting and analysis. Handling specimens in this way minimized shrinkage (Theilacker 1980) and physical damage due to net capture (McGurk 1985).

Two species of clupeid larvae were collected from samples taken in the Breakwater Marina. These species were identified as *H. castelnaui* and *Escualosa thoracata* in a size series of specimens collected during the sampling period. Details of the number of *H. castelnaui* larvae collected and numbers analyzed for age and growth are given in Table 1.

TABLE 1.—Summary of sampling dates in 1987, number of *Herklotsichthys castelnaui* collected and numbers subsequently used for otolith examination.

Date	No. collected	No. analyzed
24 August	71	50
29 August	18	18
07 September	40	40
15 September	20	20
21 September	85	48
28 September	45	45
05 October	278	50
13 October	239	50
19 October	82	50
27 October	31	31

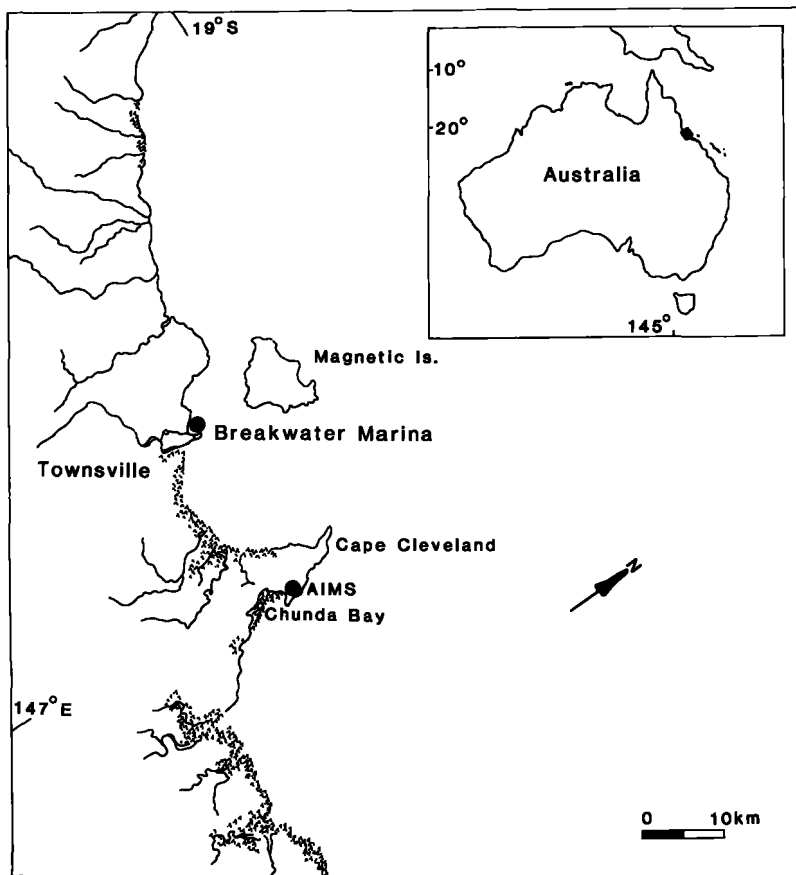


FIGURE 1.—Map of Australia showing position of Breakwater Marina, Townsville, where sampling was conducted from July to December 1987. Hatching indicates mangrove areas.

### Otolith Preparation

Standard length of larvae (tip of snout to hypural crease or tip of notochord in preflexion larvae) was measured under a stereo dissecting microscope with an ocular micrometer. Measurement was made to the nearest micrometer unit (0.135 mm at 10 $\times$  magnification). Specimens were placed in a drop of water on a microscope slide and otoliths were teased out with electrolytically sharpened tungsten needles. The larva was removed from the slide, and the otoliths air dried. To ensure dehydration, a drop of 98% ethanol was added to the otoliths and allowed to evaporate. Otoliths were then mounted in immersion oil for microscopic examination.

Individuals of *H. castelnaui* have three pairs of otoliths: sagittae, asterisci, and lapilli. Sagittae were the only otoliths found to be deposited during the

first days of larval life, and subsequently only sagittae were considered in the analysis. Growth increments were visible in sagittae from larvae that ranged from 5 to 25 mm SL. These otoliths were viewed for counting under a compound microscope using polarized transmitted light. All counts were made at 1000 $\times$  magnification. An Ikegami<sup>3</sup> high resolution video camera was mounted on the microscope, which was connected in turn to a video screen. Otolith increments were counted on the video screen as the increased contrast made rings easier to read. The system was interfaced with a Commodore Amiga personal computer for measurement of otolith radius and growth increment widths (Thorrold, MS in prep.). Otolith radius was measured from the center of the primordium to the outside

<sup>3</sup>Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

edge of the otolith, through the longest axis. Three counts were made of each sagitta, and the mean increment count from a pair of sagittae was used in the analysis. Otoliths were rejected if incremental counts within or between pairs of sagittae differed by more than two.

### Validation of Ageing Technique

To determine if the increments observed in the otoliths of *H. castelnaui* were deposited daily, larvae collected from the marina were treated with tetracycline. Tetracycline is an antibiotic that is incorporated into calcium structures of fish during growth. This can be restricted to a single day's increment on the otolith (Tsukamoto 1985), and thus, the date of treatment can be accurately identified. This technique has become widely used in the validation of ageing techniques (e.g., Campana and Neilson 1982; Schmitt 1984; Kingsford and Milicich 1987).

Larvae were collected from Breakwater Marina on 14th of October 1987 and were transported to the laboratory at the Australian Institute of Marine Science (AIMS). The fish were kept in ambient photoperiod and temperature regimes for two days to allow time for acclimation. They were fed twice daily on wild zooplankton captured with a 15  $\mu$ m mesh plankton net from Chunda Bay, adjacent to AIMS.

Ten fish were kept overnight in a 4 L tank treated with a 0.25 g/L tetracycline hydrochloride solution (Schmitt 1984). Four larvae died during exposure to the tetracycline. The remaining six larvae were returned to a 120 L tank and fed as before for 10 nights and 11 days before being sacrificed. Sagittae were dissected out of the remaining larvae and viewed under fluorescent UV and natural light with a compound microscope. Under fluorescent light an ocular marker was aligned with the fluorescent band in the otolith. The otolith was then examined under natural light, and the number of increments between the marker and the otolith margin counted. Both sagittae for each fish were analyzed, and three counts were made of each otolith.

### Statistical Procedures

Laird-Gompertz and von Bertalanffy growth models were fitted to the length-at-age data. Both models have been shown to provide adequate fits to length-age data of 0+ fish in different situations (e.g., Ralston 1976; Laroche et al. 1982). Zweifel and Lasker (1976) presented a detailed discussion of the

Laird-Gompertz function. The generalized equation of the model is

$$L_t = L_0 \exp[A_0/\alpha(1 - e^{-\alpha t})]$$

where  $L_t$  = length (mm) at age  $t$ ;  $L_0$  = length at  $t = 0$ ;  $A_0$  = specific growth rate at  $t = 0$ ; and  $\alpha$  = rate of exponential decay. Gallucci and Quinn's (1979) version of the von Bertalanffy equation was used, where the generalized equation of the model is

$$L_t = \omega/k \{1 - \exp[-k(t - t_0)]\}$$

where  $k$  = growth constant;  $L_\infty$  = maximum larval size obtained;  $\omega = kL_\infty$ ; and  $t_0$  =  $x$ -axis intercept.

The BMDP P3R<sup>4</sup> nonlinear least-squares regression program employing a modified Gauss-Newton algorithm was used to fit both models. A measure of goodness-of-fit was provided by calculating an  $r^2$  value from residual and explained sums of squares derived from the least-squares regression. Goodness-of-fit can also be assessed by examination of standard errors and approximate 95% confidence intervals of parameter estimates.

Spawning frequency of *H. castelnaui* during the sampling period was estimated by ageing larvae and then back-calculating birthdates from the time of capture. Periodicity in spawning was analyzed using the SYSTAT SERIES<sup>5</sup> program, employing an autoregressive moving average (ARIMA) model (Box and Jenkins 1976). Autocorrelation of each value in a series with every other value will define relationships between all points in the series. A plot of partial autocorrelations will detect dependencies in the data, and identify the period of any dependency.

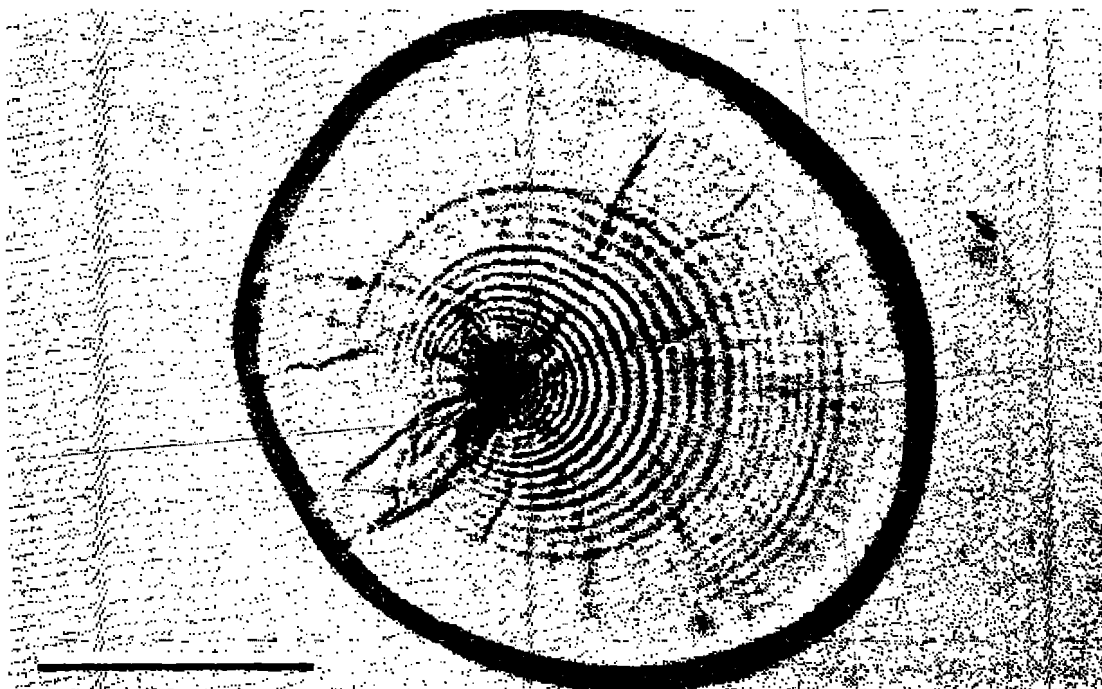
## RESULTS

### Otolith Morphology

Growth increments were clearly visible in sagittae of larval *H. castelnaui*. No marked changes in increment morphology was evident, although in some otoliths a narrowing and subsequent widening of increments occurred between increments 15 and 25 (Fig. 2). Counts of growth increments were obtained from 378 larvae ranging from 5.6 to 22.5

<sup>4</sup>BMDP 3R. 1983. BMDP statistical software. Univ. Calif. Press, Berkeley, CA 94720.

<sup>5</sup>SYSTAT SERIES. 1986. SYSTAT: The system for statistics. Evanston, IL 50201.



A



B

FIGURE 2.—*Herklotsichthys castelnaui*. Sagittae from larval herring showing daily growth increments of a 29 d old larva, 16.9 mm SL at (A) 250 $\times$  (scale bar = 0.1 mm) and (B) 1000 $\times$  (scale bar = 0.025 mm).

mm SL (see Figure 4), and from estimated ages of 3–53 days old. The increments were easily read in most otoliths; only 24 larvae were rejected due to either the error in reading precision being greater than 2 for the sagittae of a larva (10, 2.5%) or because otoliths could not be clearly read (14, 3.5%).

The plot of standard length (SL) against sagittae maximum radius (OD) revealed a logarithmic relationship (Fig. 3). Otolith diameter data were  $\log_e$  transformed, and a regression equation fitted to the transformed data. This equation is described by

$$SL = 5.61 \cdot \log_e OD - 10.56$$

$$(n = 378; F = 2156; P < 0.0001; r^2 = 0.85).$$

Comparison of means from observed and predicted standard length values suggested that any bias caused by  $\log_e$ -transforming otolith diameter was negligible.

### Validation of Ageing Technique

Increments were deposited daily in the sagittae of the six larval *H. castelnaui* kept under ambient conditions in the laboratory (Table 2). When viewed under natural light, a mean of 10 increments were visible from the fluorescent band to the margin of the sagittae. This corresponded to the number of nights that the fish were held after the tetracycline treatment.

### Larval Age and Growth

It was assumed that the first otolith increment was laid down at hatching (see Discussion); therefore, the age of *H. castelnaui* larvae was estimated directly from the number of growth increments in the sagittae. Ages were thus minimum estimates for any given length. Descriptions of growth of larval *H. castelnaui* were based on age-at-length of 378

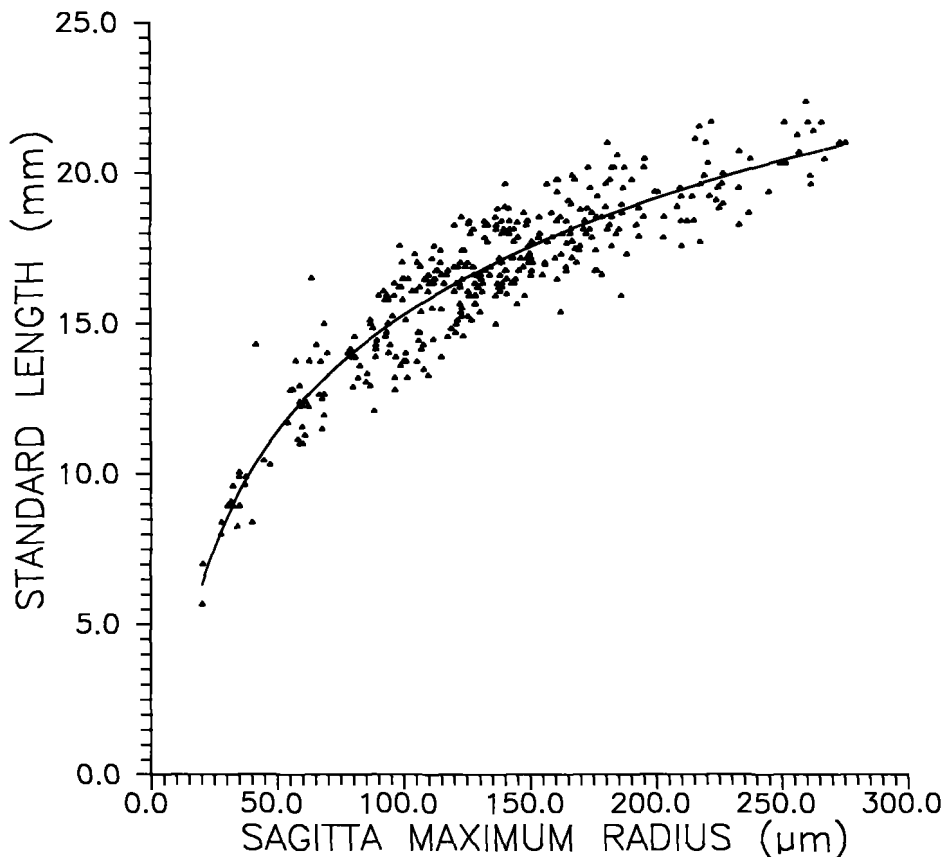


FIGURE 3.—Relationship between standard length and radius of sagittae for larval *Herklotsichthys castelnaui*, together with fitted logarithmic growth curve.

specimens, 5.6–22.5 mm SL. Laird-Gompertz and von Bertalanffy models yielded good and nearly identical fits to the data ( $r^2 = 0.74$  for the Laird-Gompertz curve,  $r^2 = 0.75$  for the von Bertalanffy

curve); therefore, only the Laird-Gompertz growth curve is presented (Table 3; Fig. 4). This relationship does, however, appear to underestimate growth at ages less than 10. By contrast, the von Bertalanffy curve underestimated growth at ages greater than 38.

TABLE 2.—Validation of ageing using the tetracycline technique. Fish were preserved 11 days after treatment with tetracycline. Table shows standard length (SL), mean number of increments observed between the fluorescent band and the margin of both sagittae ( $\pm$  standard error), and the range of increment counts on each of the six fish.

Fish no.	SL	Mean $\pm$ SE	Range
1	20.6	9.5 $\pm$ 0.2	9–10
2	21.5	10 $\pm$ 0.5	9–11
3	21.0	10 $\pm$ 0	10
4	22.6	10.3 $\pm$ 0.2	10–11
5	22.6	10 $\pm$ 0.4	10–11
6	20.6	10 $\pm$ 0	10
Total		9.8 $\pm$ 0.1	9–11

TABLE 3.—Laird-Gompertz equation and estimated parameters describing growth of 378 *Herklotsichthys castelnaui* larvae. The growth model was fitted using nonlinear least-squares regression. STDERR = asymptotic standard error of parameter estimates; C.L. = approximate confidence intervals of parameter estimates.

Equation		
$L_t = 5.159 \exp[0.104/0.075 (1 - e^{-0.075t})]$		
Parameters	STDERR	95% C.L.
$L_0 = 5.159$	0.348	$L_1 = 4.474, L_2 = 5.843$
$A_0 = 0.104$	0.011	$L_1 = 0.082, L_2 = 0.125$
$\sigma = 0.075$	0.0054	$L_1 = 0.064, L_2 = 0.086$

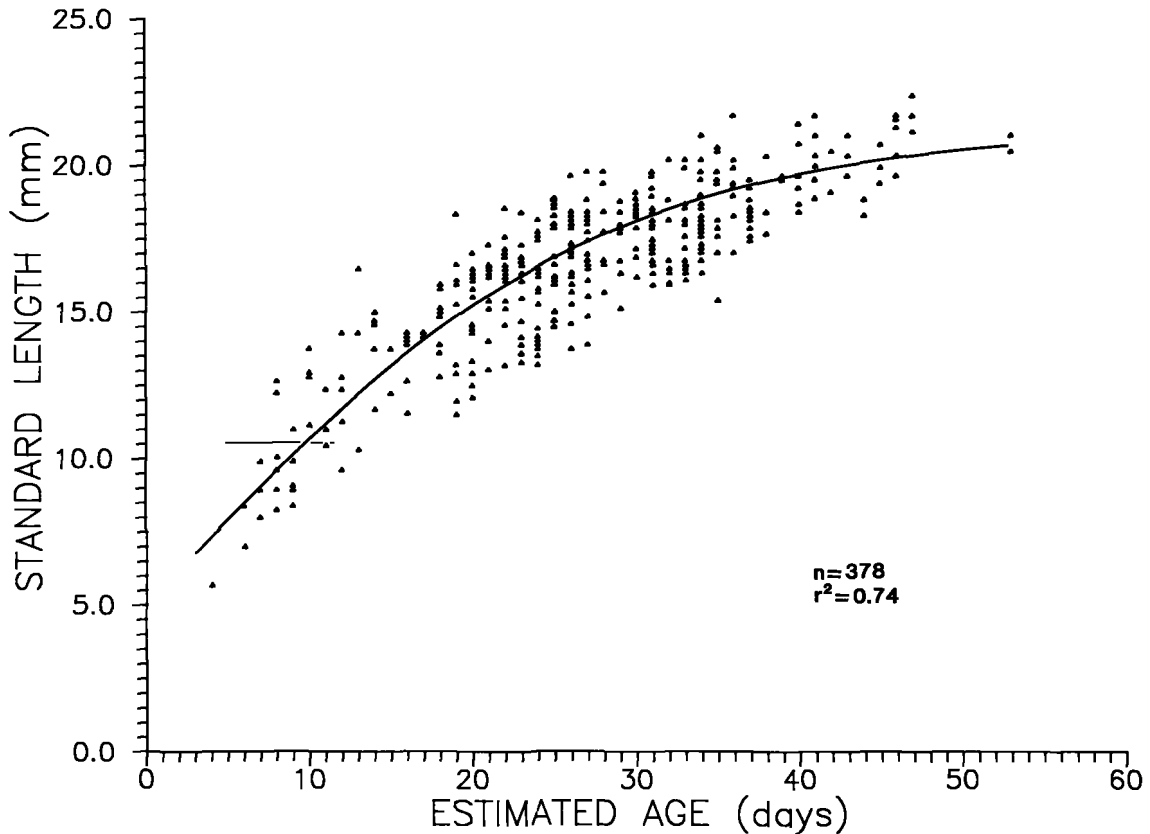


FIGURE 4.—Relationship between standard length and number of growth increments (increment number) on sagittae for larval *Herklotsichthys castelnaui*, together with fitted Laird-Gompertz growth curve.

Estimates of specific and absolute growth rates (Table 4) were calculated from length-at-age ( $L_t$ ) for various ages as predicted by the Laird-Gompertz equation

$$L_t = 5.26 \exp[0.104/0.075 (1 - e^{-0.075t})].$$

Specific growth rate declined from 7.4% to 1.1% per day SL at 30 days after hatching, before leveling off at around 0.5% per day SL over the latter half of larval life. Absolute growth showed a similar pattern, with a rapid decline from a maximum value of 0.57 mm/d at day 5 to a value of approximately 0.1 mm/d approaching metamorphosis, 40–50 days after hatching.

Spawning occurred over three months (mid-July to mid-October), peaking around the first week in September (Fig. 5). There are indications of lunar periodicity within those months; spawning peaks were separated by approximately two weeks, apparently associated with first and third quarter moon phases. Time series analysis also indicated a 14 d periodicity in spawning peaks. Autocorrelation coefficients larger than two standard errors of the mean autocorrelation coefficient are considered significant (fn. 5). Coefficients greater than this value

TABLE 4.—Growth rates of *Herklotsichthys castelnaui* larvae predicted from the Laird-Gompertz growth equation at various times after hatching.

Age (days)	Specific growth rate (%/d SL)	Absolute growth rate (mm/d)
4–5	7.4	0.57
9–10	5.1	0.53
14–15	3.5	0.45
19–20	2.4	0.36
24–25	1.7	0.27
30–31	1.1	0.20
34–35	0.8	0.15
40–41	0.5	0.10
44–45	0.4	0.08

(0.29) occurred on day 0 (0.62) and day 14 (0.39), indicating the existence of a periodicity in the data of 14 days.

## DISCUSSION

Clear growth increments consisting of alternating light and dark bands were visible in all three pairs of otoliths in *Herklotsichthys castelnaui*. Asterisci and lapilli were formed, however, some time after the sagittae. This suggested that the number of

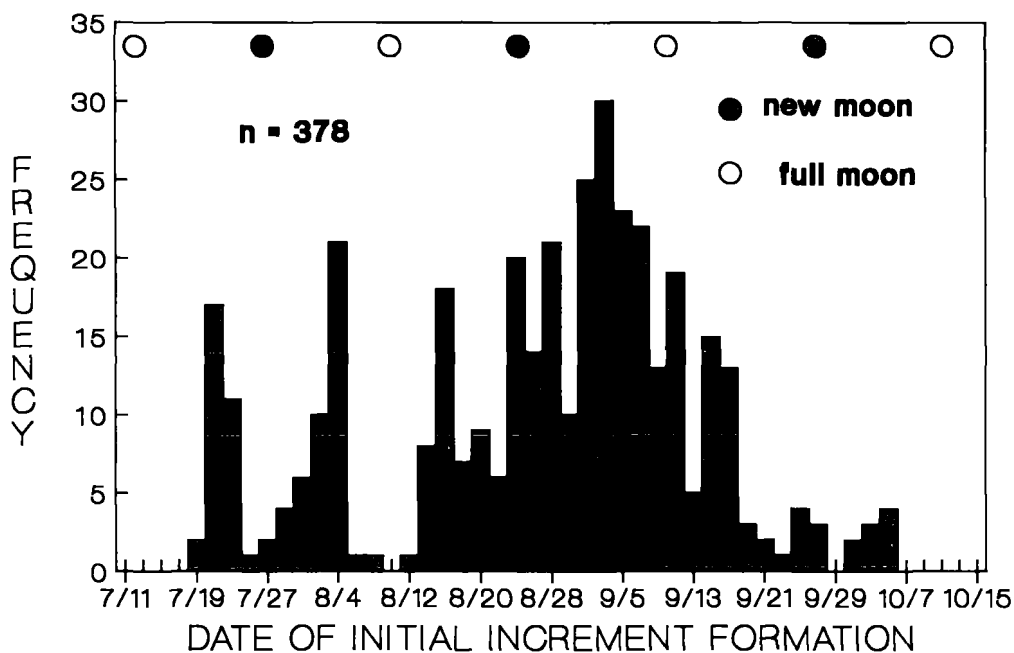


FIGURE 5.—Spawning periodicity of *Herklotsichthys castelnaui* based on back-calculated dates of initial increment formation. Frequency values are 2 d class means, two increments being the maximum accepted error in increment counts.



growth increments on the sagitta provided the closest estimate of age in larval *H. castelnaui*.

Age at initial increment deposition was not determined in this study. Initial growth increments have been shown to be deposited prior to egg hatching, at hatching, just after hatching, and at onset of exogenous feeding (Brothers et al. 1976; McGurk 1984; Kingsford and Milicich 1987). All temperate clupeids studied have initiated ring formation at yolk-sac absorption (Geffen 1982; Lough et al. 1982; McGurk 1984; Re 1984) from 3 to 5 days after hatching. Although no work has been published on otolith formation in tropical clupeids, a comparatively high water temperature, and hence a rapid developmental rate, suggests that endogenous reserves would be quickly exhausted (Houde 1974). It was thus assumed here that the first otolith increment is laid down at hatching, and otolith counts were assumed to be a direct measure of age. Violation of this assumption will have led to biased estimates of  $L_0$ , the size at hatching, and  $A_0$ , the specific growth rate at hatching, in the Laird-Gompertz model. The magnitude of absolute and specific growth rates remain valid. The age at which the growth rates were calculated will, however, have a systematic error corresponding to the time from hatching to initial increment formation.

Standard length increased as a logarithmic function of otolith radius. Linear (e.g., Rice et al. 1985), logarithmic (Nishimura and Yamada 1984; Tsuji and Aoyama 1982), and some combination of the two functions (Jenkins 1987) have been reported in the literature. A close correlation between standard length and otolith growth at a daily level implies that the width of any growth increment is a measure of instantaneous growth (Campana and Neilson 1985). The smoothly monotonic relationship between standard length and otolith radius presented here suggests that it may be valid to reconstruct individual growth histories by examination of growth increment spacings in sagittae of *H. castelnaui*.

Both Laird-Gompertz and von Bertalanffy growth curves adequately fitted the length-at-age data. The growth trajectory of larval *H. castelnaui* indicates that growth is rapid for the first two to three weeks, but slows after this period. Growth may become asymptotic after this point, as predicted by the single cycle Laird-Gompertz model, or alternatively, enter a new growth stanza during juvenile life, as has been reported for *Herklotsichthys quadrimaculatus* (Williams and Clarke 1983).

Data presented here for larval *H. castelnaui* affords good comparison with some temperate clupeid species, where growth rates have also been elu-

cidated using the otolith increment technique. Initial growth rates of 0.5–0.6 mm/d in *H. castelnaui* are as high as any recorded for clupeid larvae in the field. Similar growth estimates have been reported off South West Africa, where *Sardinops ocellatus* larvae grow linearly at rates of approximately 0.7 mm/d (Thomas 1986). Growth estimates of 0.2–0.4 mm/d after this initial burst are closer to those presented for *Clupea harengus* from the northern Atlantic (Townsend and Graham 1981; Lough et al. 1982; Henderson et al. 1984). Growth rates of larval *H. castelnaui* may reflect higher ambient water temperatures, as both *S. ocellatus* and *C. harengus* have a higher  $L_\infty$  and hence higher predicted growth rates (Ricker 1975).

Spawning periodicity in *H. castelnaui* was apparently correlated with the quarter moon phases. Lunar-synchronized spawning has been reported in salmoniform, atheriniform, tetraodontiform, and perciform fishes (Taylor 1984). Most fish species with lunar-spawning rhythms spawn on or around the new or full moon (e.g., Lobel 1978; Middaugh et al. 1984), although spawning in French grunts, *Haemulon flavolineatum*, also appears to be coupled with quarter moons (MacFarland et al. 1985). It should be noted that results presented here may be subject to some systematic error in ageing. If, for example, initial increment formation occurs some time after hatching, then birth dates will have been consistently underestimated. MacFarland et al. (1985) hypothesized that currents favorable for settlement may account for fertilization and recruitment events peaking on the quarter moon. My results suggest that spawning occurs with some semilunar periodicity, but the time of initial formation needs to be determined before relating spawning events to moon phases and possible tidal influences on egg and larval distributions.

The most significant advantage of using otolith ageing techniques is the ability to produce individual rather than population statistics. Although it has been possible to fit a growth equation to the length-age data presented here, there is also an amount of variability surrounding the curve. This variability may, at least in part, be a sampling artifact caused by methodological problems. Inaccurate age determinations may be caused by nondaily deposition of rings under some conditions (e.g., Geffen 1982), or failure to detect all rings within an otolith due to the resolution problems of light microscopy (Campana et al. 1987). Conversely, if the data are accurate, variable growth rates on small spatial (tens of meters) and temporal (days) scales are detectable by otolith analysis. It is often tacitly assumed in lar-

val studies that a fast growth rate will be reflected in lower mortality rates, although the implications of fast or slow growth to subsequent survivorship have yet to be addressed. Otolith analysis emphasizing individual rather than population growth parameters may provide a tool for approaching such questions in field situations.

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